FACTORS AFFECTING THE ESCAPE BEHAVIOUR OF A RIPARIAN LIZARD

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The escape tactics employed by water skinks, *Eulamprus quoyii*, are determined by their immediate location and orientation and by the physical characteristics of the habitat. Running was the most frequently practised type of escape, with rocks the preferred form of cover. Swimming and diving were employed to a lesser extent. Juvenile water skinks did not differ in escape behaviour from adults.

Water skinks use only a small proportion of their maximal locomotor and diving abilities during escape. Short dives and/or short bursts of swimming or running enable escape from a predator and still allow the individual to resume normal activities almost immediately (or execute more evasive manoeuvres). Juveniles are poorer swimmers and divers but only slightly poorer runners than adults.☐ *Eulamprus quoyii, escape diversity, running, swimming, diving, micohabitat.*

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The selection of an appropriate escape response is a critical factor in survival, and recently has been analysed using lizards as model animals (Jaksic and Núñez, 1979; Simbotwe, 1983; Schall and Pianka, 1980). The latter found that lizards alternated among various methods of escape, and predicted that prey populations faced with higher per capita predation pressure should evolve more diverse escape tactics than less heavily predated conspecific populations. The present paper deals with the more proximate nature of diversity and escape tactics, by asking the following question: When a lizard is threatened, what factors determine which of the escape tactics in its repertory it will use? The subject of the study was the water skink *Eulamprus quoyii* (formerly *Sphenomorphus quoyii*), a riparian lizard that eludes predators by running to terrestrial cover, and/or by swimming or diving (Veron and Heatwole, 1970).

STUDY AREAS

The study was undertaken at three locations near Armidale, NSW, Australia, in summer (January and February) 1983. Each site comprised 1.5km of stream bank. They were structurally different but all supported large populations of water skinks. The heterogeneity of each habitat was determined by quantifying the emergent ground cover in 10 m^2 sections every 100m along the stream bank. The percentage of each section covered with small rocks (surface area<15cm^2), medium-sized rocks (15-100cm^2), large rocks (>100cm^2), vegetation and fallen timber, and bare ground, was recorded. Rocks 15-100cm^2 seemed to be optimal basking sites. Stream speed was measured at each section by timing the rate of passage of a floating ball down the fastest flowing 10m. The characteristics of the three sites are presented in Table 1.

Boorolong Creek, 26km southwest of Armidale, was a wide, slowly flowing stream usually divided into very large pools by granite outcrops or fallen trees; the banks were densely lined with reeds, grasses, blackberries (*Rubus* sp.) and *Casuarina*. The Gara River, 15km north of Armidale, was a narrow, rapid stream with many small pools located at the periphery. The stream contained many large rock outcrops but small rocks were comparatively scarce. The banks were densely lined with reeds, grasses and bottlebrushes (*Callistemon* sp.). Blue Hole was located 15km downstream from the Gara River study site and 15km northwest of Armidale. The banks were thickly covered with granite boulders of a variety of sizes with a corresponding reduction in streamside vegetation. Although

TABLE 1. Characteristics of the three streams used as study sites expressed as $\bar{x}$% ± S.E. (n).

MICROHABITAT	BLUE HOLE	GARA RIVER	BOOROLONG CREEK
Open Bank	13.1± 3.6 (12)	31.3± 6.4 (10)	33.9± 6.5 (15)
Small rocks	9.4± 2.2 (12)	1.5± 1.1 (10)	19.3± 4.4 (15)
Medium sized rocks	15.8± 2.3 (12)	6.5± 1.5 (10)	10.0± 3.7 (15)
Large rocks	53.3± 5.0 (12)	5.7± 2.2 (10)	6.9± 2.2 (15)
Vegetation	7.5± 1.4 (12)	55.0± 6.8 (10)	30.3± 6.4 (15)
Flow rate (ms^{-1})	1.3± 1.8 (12)	0.73± 0.19(10)	0.10± 0.05(15)

midstream flow is rapid, the rocks allow the formation of numerous small, quiet pools. The vegetation consisted primarily of grasses, blackberries and casuarinas. All sites were located in dry sclerophyll forest or open woodlands. In summary, Blue Hole was much rockier, more open and less vegetated than the other two sites, and Gara River had a higher rate of stream flow than the other two.

MATERIAL AND METHODS

ECOLOGICAL FACTORS

Observations were undertaken only on fine sunny days with little or no wind and air temperature of 25-30°C. Light falls of rain occurred intermittently during the study period but were not sufficient to greatly alter stream morphology or rate of flow.

The stimulus used to induce escape was a person approaching on foot at a moderate speed from the landward side. The same person was used throughout. For each escape event the following data were recorded: (1) initial microhabitats and body orientation of the lizard with respect to the water and to bank cover, (2) execution of changes in direction from the initial orientation, but prior to fleeing, (3) microhabitat selected for escape and (4) escape tactic employed. Data from adults and juveniles were recorded separately; juveniles were defined as water skinks shorter than 85 mm snout to vent (Veron, 1969).

The categories of initial microhabitat were: (1) water, (2) on a rock surrounded by water, (3) on a rock on the bank and (4) on the bank.

A lizard's initial orientation was tallied as (1) facing the water, (2) facing the bank or (3) parallel with both. Alteration in orientation prior to fleeing was listed as nearest to 0°, 45°, 90°, 135°, or 180° from original orientation.

The covers selected for protection were classed as (1) reeds, (2) rocks, (3) the bank or (4) open water.

Water skinks utilised terrestrial (running), or aquatic (swimming and/or diving) escape tactics. Swimming was always undertaken on the surface with the head above water, while diving was defined as a descent to the bottom of a pond and remaining motionless there in leaf litter or rock crevices, usually for several minutes. Occasionally lizards did not move when approached and were easily caught. Another escape response, active surface swimming followed by a dive, was only occasionally observed and represents the only overlapping of categories of escape tactics.

Values for the breadth of each habitat niche were calculated using Simpson's (1949) diversity index (DS). Microhabitat niche overlap and escape behaviour overlap were calculated using Pianka's (1973) index. Statistical analyses employed the chi-squared goodness of fit and the G test for independent samples (Sokal and Rohlf, 1969; Snedecor and Cochrane, 1978).

Since observations were made at different times of day, a test was made to see whether there was a temporal effect. Morning and afternoon values were not significantly different for microhabitats prior to escape (G = 0.86; P>0.05; niche overlap between morning and afternoon = 0.999), escape tactic (G = 4.26; P>0.05), original orientation (G=1.24; P> 0.05) and degree change in orientation (G = 4.10; P>0.05). Consequently, data from both periods of the day were pooled for subsequent analyses.

Data on microhabitat prior to escape were also pooled for juvenile and adult lizards as at all sites there were no significant differences between the age classes (G = 1.94, 5.40, and 6.80 for Blue Hole, Gara River and Boorolong Creek respectively; P>0.05 in all cases; niche overlap between juveniles and adults in the three respective areas were 0.988, 0.922 and 0.938). There were too few juveniles for testing the other results for Gara River. However, there were no significant differences between adults and juveniles in escape tactics (G = 5.12 and 5.64 for Blue Hole and Boorolong Creek respectively, $P>0.05$ in both cases) original orientation (G = 1.96 and 0.94; $P>0.05$) and degree change in orientation (G = 2.28, 4.34; $P>0.05$), and data were pooled for these as well.

PHYSIOLOGICAL FACTORS

Eulamprus quoyii were tested to determine voluntary diving time, swimming speed, stamina, running speed and running stamina according to methods already described (Daniels, 1984b, 1985). Lizards were collected by hand from Tea Tree Creek and Boorolong Creek between February 1982 and December 1983. Adults and juveniles were both maintained as previously described (Daniels, 1984b, 1985). In the experiments, unless otherwise stated, air temperatures of 30-32° and water temperatures of 19-20°C were used. These temperatures approximate air and water temperatures during summer at creeks inhabited by the species (Pidgeon, 1978) and straddle its mean preferred body temperature of 29.6°C (Spellerberg, 1972a,c).

Diving time determined by timing 30 dives for each of 21 lizards at a water temperature (mean ± S.D.) of 19.1° ± 1.7°C and an air temperature of 31.6° ± 1.1°C. Swimming stamina was examined by maximally exercising 16 lizards until exhaustion (trial 1). The time taken before the lizard stopped swimming was recorded. A second swimming trial (trial 2) was conducted on the same lizard 20 minutes later to determine recovery capacity. Two trials per lizard were conducted every day for 10 days. Running speeds were determined by stimulating 17 lizards to run the length of a 161 x 40 x 50cm glass tank with a sand substrate at Ta = 31.6° ± 1.1° C. Ten trials were conducted for each lizard with 20 minutes rest between trials. Juvenile *E. quoyii* were timed while running a distance of 68cm. Running stamina was also determined at an ambient temperature of 18.1° ± 0.8°C in a tank (24.5 x 38.5 x 37.5cm) with a dirt substrate. Nine lizards were chased, one at a time, around the periphery of the tank until they refused to move after five consecutive taps on the base of the tail. A low ambient temperature was chosen to match that of the water temperature during the swimming stamina experiments, so as to make direct comparisons between the two types of stamina possible. A second running endurance trial was conducted for each lizard 20 minutes after the first; two such trials were conducted each day for 10 days.

All times were recorded using a Lauris Stopwatch accurate to 0.02 seconds. From the repetitions of all experiments mean values were calculated for each individual; the maximum value was also analysed. All results were expressed as means ± standard errors (S.E.) except air and water temperatures which were expressed as means ± standard deviations (S.D.). Statistical analysis employed Student t-test and paired t-tests (Sokal and Rohlf, 1969). Speeds were expressed in metres per second (ms^{-1}), and stamina and diving times were expressed in seconds (s). In addition to these laboratory studies, voluntary diving, swimming and running times were determined in the field. Water skinks were chased into the water at Blue Hole and Boorolong Creek and timed till they swam to cover or, if they dived, until re-emergence. Air and water temperatures were recorded at the site of entry into the water. Running times were recorded at Blue Hole and Boorolong Creek for lizards chased from their basking sites towards rocks or reeds. Air temperatures were recorded at the basking sites.

RESULTS

MICROHABITAT

Undisturbed water skinks were usually at sunlit sites, particularly on rocks near the water (Table 2). The second highest usage was of the stream bank. Only occasionally were lizards in the water, floating or resting on algal mats. Thus, there seems to be a clear preference for emergent streamside sites rather than for the water itself. There were three major terrestrial microhabitats available, rocks, open banks and vegetation (Table 1). When the observed frequencies of their use by lizards were tested by Chi-square analysis against the values expected on the basis of their relative cover, the observed values departed significantly from the expected ones (X^2, Blue Hole 54.1, Gara River 298.0, Boorolong Creek 86.4; $P<<0.005$ in all cases), indicating the lizards were not randomly associated with substrate type. No lizards were found in the vegetation at any locality despite it having mean cover values in the three areas of 7.5-55.0% but rocks and open habitats had rather high frequencies of usage. Thus, the lizards seemed to select non-vegetated microhabitats.

TABLE 2. Microhabitat preferences (frequency of use) of *Eulamprus quoyii* prior to escape.

MICROHABITAT	BLUE HOLE	GARA RIVER	BOOROLONG CREEK
In water	0.015	0.048	0.039
On rock in water	0.111	0.136	0.196
On rock on bank	0.637	0.552	0.324
On bank	0.237	0.264	0.441
n	333	124	204
X^2(df)	1.62 (1)	188.86 (1)	2.19 (1)
P	>0.05	<0.05	>0.05
Niche breadth	0.369	0.510	0,649

To test whether rock or open banks were favoured, a second Chi-square analysis was performed testing observed frequencies of use of these microhabitats relative to their proportional representation in non-vegetated stream sides. At Blue Hole where rocky habitat was abundant and bare bank relatively rare (Table 1) the lizards inhabited banks more often than expected by its relative cover ($X^2 = 25.4$; $P << 0.005$). At the Gara River where open bank was well represented and rocks less common, the lizards favoured rocks ($X^2 = 96.0$, $P << 0.005$).

At Boorolong Creek where the two microhabitats were represented in about equal proportions, use of rocks and banks did not differ significantly from expected values ($X^2 = 0.51$; $0.50 > P > 0.025$). It may be that the lizards tend to preferentially use whichever is the rarer of these two microhabitats. Niche breadth was greatest at Boorolong Creek, the locality with the most even coverage of habitat types, and least at Blue Hole where habitat diversity was lowest, rocks accounting for over 78% of total microhabitat (Tables 1, 2).

Overlap in microhabitat niche was high among sites (Table 2). Gara River and Boorolong Creek, the two sites most similar in habitat characteristics (Table 1), did not differ significantly in the frequency of use of different microhabitats by the lizards (Table 3). The greater dissimilarity in habitat characteristics of Boorolong Creek was reflected in a significant difference in frequency of microhabitat use by lizards there in comparison to the other two places (Table 3).

ESCAPE BEHAVIOUR

When approached, lizards usually escaped significantly more often by running rather than by swimming or diving. Rocks were the preferred cover sought regardless of the escape route or mode of locomotion employed (Table 4). The diversity of escape responses was lowest at Blue Hole, which had the greatest uniformity of microhabitat and the greatest proportion of rocks, the preferred escape cover (Tables 1, 4).

Although the overlap in escape tactics was high among areas, each area differed significantly from every other in the frequency with which different tactics were employed, and with one exception (Gara River vs Boorolong Creek), in the frequency with which different modes of locomotion were used (Table 3). The most notable differences were that in the rockiest area (Blue Hole) lizards ran to rocks more often for escape than at the other localities, and employed aquatic escape less frequently (Table 4). In the terrestrial situation water skinks at Blue Hole employed terrestrial escape tactics significantly more often than did those from Boorolong Creek ($G_{(1)} = 11.26$; $P < 0.05$); those that originally faced parallel to or toward the banks escaped less frequently to water at Blue Hole than did those with similar initial orientation at Boorolong Creek ($G_{(1)} = 4.96$; $P < 0.05$). It would seem that when rocks are abundant they are preferentially used for escape, but when they are less abundant, escape by diving or swimming increases in frequency.

Rate of stream flow also may be a factor. Blue Hole, where aquatic escape was lowest, had the swiftest current (Table 1).

Unmolested water skinks most frequently faced the water, and once disturbed, they tended to move away in the direction they were originally facing, usually to the nearest rock (Table 5). Thus, either the lizards tended to face toward predetermined escape routes or perhaps merely

TABLE 3. Comparison among localities of the microhabitat selection and escape tactics of *Eulamprus quoyii*.

	GARA RIVER VS BOOROLONG CREEK	BOOROLONG CREEK VS BLUE HOLE	BLUE HOLE VS GARA RIVER
MICROHABITAT			
Niche overlap	0.884	0.830	0.993
G (df)	20.18 (3)	50.92 (3)	5.38 (3)
P	<0.05	<0.05	>0.05
ESCAPE TACTICS			
Overlap	0.933	0.693	0.893
G (df)	17.76 (9)	111.06 (9)	43.88 (9)
P	<0.05	<0.05	<0.05
ESCAPE TACTIC SUBTOTALS			
G (df)	3.16 (3)	20.60 (3)	10.78 (3)
P	>0.05	<0.05	<0.05

fled in whatever direction they happened to facing.

Approach was from the landward side and that may have influenced direction of escape. The 90° and 180° turns occurred most often when the lizard was initially facing the direction from which the person approached. However, a landward approach would be expected to drive the lizards into the water, rather than along terrestrial escape routes. Such did not occur and direction of approach did not seem to be an overriding factor.

Unfortunately, data on original orientation and degree change of direction are available only for two sites (Blue Hole and Boorolong Creek). These two areas did not differ in regard to the direction undisturbed lizards faced (Table 5). By contrast, those from Boorolong Creek tended to alter their original orientation in order to escape, significantly more often than did those from Blue Hole (Table 5). This is probably because the abundance of rocks at Blue Hole provided escape avenues in almost all directions, but at Boorolong Creek where rocks were less than half as abundant, a lizard would more often have to change direction in order to head for rocky cover.

Comparison of the antecedent behaviour of lizards escaping aquatically with those escaping terrestrially, revealed a number of important differences. For example, at all study sites lizards that were already in the water or on rocks surrounded by water used an aquatic avenue of escape more often than a landward escape; those initially located on land escaped significantly more often to the land than to water (Table 6). Thus, the microhabitat occupied at the time of disturbance influences the avenue of escape that is adopted.

At Boorolong Creek, lizards parallel to the shore or facing the water initially showed no significant preference for escape to any particular medium, but those facing the land effected a terrestrial escape significantly more often than they fled to water (Table 6). At Blue Hole most animals in all categories escaped to land. For those parallel to the shore or initially facing land selection for a landward escape was significant; for those originally facing water it was not (Table 6). Thus, initial orientation may influence direction of escape.

Finally, there was no significant correlation between the degree of change in direction and the proportion of escapes that were toward the water (Spearman Rank Test: Boorolong Creek $r_s = -0.6$, $P>0.10$; Blue Hole $r_s = -0.4$, $P>0.10$). The data (Table 6) again confirmed the greater tendency toward terrestrial escapes at Blue Hole compared to Boorolong Creek. In neither area, however, are lizards that escaped in the direction they initially faced more (or less) prone to escape toward a particular medium than are those which showed greater amounts of turning after disturbance.

LOCOMOTOR PERFORMANCE

Adult and juvenile *Eulamprus quoyii* both exhibited similar diving behaviours. Lizards often submerged vertically in a crevice in the diving tank, and remained motionless with eyes closed throughout the dive. Both size groups exhibited a mean voluntary diving time in the laboratory

TABLE 4. Escape tactics of *Eulamprus quoyii* at three sites.

ESCAPE TACTIC	BLUE HOLE	GARA RIVER	BOOROLONG CREEK
Swim : to Reeds	0.034	0.134	0.188
: to Rocks	0.197	0.119	0.127
: to Bank	0.040	0.060	0.075
: then Dive	0.003	0.022	0
Dive : in Open Water	0.003	0.007	0.014
: in Reeds	0.009	0.015	0.028
: in Rocks	0.017	0.045	0.042
Run : to Rocks	0.519	0.299	0.174
: to Reeds	0.165	0.254	0.333
Remain Motionless	0.014	0.045	0.019
n	351	134	213
X^2 (df)	137.74(9)	165.50(9)	157.82(9)
P	<0.05	<0.05	<0.05
Escape Diversity	2.95	5.14	4.97
ESCAPE TACTIC SUBTOTALS			
Swim	0.274	0.336	0.390
Dive	0.028	0.067	0.085
Run	0.684	0.552	0.507
Remain Motionless	0.014	0.045	0.019

of between 5 and 6 minutes (Table 7), and the difference between the two groups was not significant ($t_{(19)} = 0.65$, $P>0.05$). However, the adults did have significantly longer maximum dives ($t_{(19)} = 1.86$, $P<0.05$). The longest dive for an adult *E. quoyii* was 35.4 minutes and the longest dive by a juvenile was 15.1 minutes. There was a significant trend in both groups for mean voluntary dive time to decrease as the number of completed dives increased (Daniels, 1984a,b, 1985). In the field, water skinks dived for only short periods. Mean voluntary diving time was 2.5 ± 2.00 minutes (n = 12) with the longest dive being 12.5 minutes (water temperature 24.1°+ 0.51°C; air temperature 28.2° ± 0.87°C).

The skinks usually swam in an anguilliform manner (Batholomew et al., 1976). The legs were held laterally against the side of the body and thrust was developed by lateral undulations of the body and tail. As the lizards became exhausted, tail undulations became weaker and propulsion was maintained by body movements and, prior to complete exhaustion, with flipper-like actions of the forelegs. The size groups exhibited significantly different mean speeds ($t_{(15)} = 85.37$, $P<0.05$) and maximum speeds ($t_{(15)} = 122.77$, $P<0.05$) (Table 11). The fastest adult *S. quoyii* swam at 1.34ms^{-1} and the fastest juvenile at 0.4ms^{-1}. In the first swimming trial, lizards continued swimming for more than two minutes. Juveniles had slightly less stamina (mean swimming stamina: $t_{(14)} = 1.10$, $P>0.05$). The longest endurance for an adult in trial 1 was 181s and for a juvenile 163s.

If adult water skinks could sustain a mean swimming speed of 0.64ms^{-1} for two minutes, then they could swim up to 80m before becoming exhausted. However, 124 adults and juveniles inhabiting New England creeks and chased into water of 21.0 ± 0.86°C (air temperature 23.5 + 1.09°C) swam for 2.19 ± 0.15s, with the maximum swimming period being 79.5s. There was no significant difference in these swimming times between adults and juveniles(adults: 3.69 ± 0.96s, n = 88; juveniles: 1.65 ± 0.19s, n = 36; Student t- test: $t_{(122)} = 1.37$, $P>0.05$). Lizards rarely swam more than 2-3m before emerging onto rocks or the bank.

Twenty minutes after being exercised maximally, lizards could only sustain short bursts of swimming (Table 7). Mean swimming stamina was significantly less in trial 2 than in trial 1 for both groups (adults: $t_{(205)}= 20.73$, $P<0.05$; juveniles: $t_{(101)} = 13.39$, $P<0.05$). The greatest stamina for an adult in trial 2 was 121s and for a juvenile 100s. Adults swam for significantly longer than juveniles in trial 2 (mean stamina:

TABLE 5. Original orientation and degree change in direction by *Eulamprus quoyii* from Blue Hole and Boorolong Creek.

	BLUE HOLE	BOOROLONG CREEK
ORIGINAL ORIENTATION		
Facing Water	0.407	0.354
Parallel to Water/Bank	0.258	0.323
Facing Bank	0.335	0.323
n	248	201
X^2 (df)	38.15(2)	25.44(2)
P	<0.05	<0.05
G (df)	2.54(2)	
P	>0.05	
DEGREE CHANGE IN DIRECTION		
0°	0.421	o 373
45°	0.109	0.070
90°	0.239	0.294
135°	0.065	0.080
180°	0.166	0.184
n	247	201
X^2 (df)	91.802(4)	73.654(4)
P	<0.05	<0.05
G (df)	4.4(4)	
P	<0.05	

$t_{(14)}$ = 2.28, P<0.05; maximum stamina: $t_{(14)}$ = 2.78, P<0.05).

The intraspecific differences observed for swimming stamina were not observed for running stamina (Table 7). Juveniles could sustain activity for as long as adults in trial 1 (mean running stamina: $t_{(7)}$ = 0.45, P> 0.05; maximum stamina : $t_{(7)}$ = 0.21, P>0.05). Maximum running endurance for an adult in trial 1 was 142s and for a juvenile 144s. Adults and juveniles also possessed similar recovery capacities (Table 7) (mean running stamina in trial 2: $t_{(7)}$ = 1.05, P>0.05; maximum stamina $t_{(7)}$ = 0.42, P> 0.05). During trial 2 the longest endurance of an adult was 103s and that for a juvenile was 108s. As in the swimming stamina trials, the mean exercise times in trial 2 were significantly shorter than those of trial 1 (adults, $t_{(43)}$ = 12.47, P<0.05; juveniles, $t_{(38)}$ = 13.00, P<0.05). No significant differences existed between the mean running and swimming stamina of adults (trial 1: $t_{(151)}$ = 1.65; P>0.05; trial 2: $t_{(140)}$ = 1.66; P>0.05). Juveniles swam longer than they ran in trial 1 ($t_{(98)}$ = 2.56, P<0.05).

Adults ran faster than hatchlings (Table 7), (mean speed: $t_{(15)}$ = 27.89, P<0.05; maximum speed $t_{(15)}$ = 34.78, P<0.05). The fastest speed for an adult was 1.52ms^{-1} and that for a juvenile was 0.76ms^{-1}. When approached in the field, lizards utilised only short bursts of running. The mean time it took lizards to reach cover, once disturbed, was 1.90 ± 0.80s (n = 56) (air temperature = 28.2° ± 0.87°C.

DISCUSSION

DIVERSITY OF ESCAPE TACTICS

Water skinks are potential prey for over 100 different species of vertebrate predators (Daniels and Heatwole, 1984), yet they exhibited a relatively low index of escape diversity. The values of 2.95-5.14 (Table 4) rank in the bottom third of the 14 species of lizards so far studied (Table 8). The small diversity value reflects the high proportion of individuals that retreated to a single type of cover (rocks). It may be that such a tactic is effective against a wide range of the common predators of water skinks. Another pos-

TABLE 6.Percentage of aquatic and terrestial escapes of *Eulamprus quoyii* to microhabitat selection, original orientation and degree change in direction.

	BLUE HOLE			GARA RIVER			BOOROLONG CREEK		
	AQUATIC	TERRESTRIAL	N	AQUATIC	TERRESTRIAL	N	AQUATIC	TERRESTRIAL	N
MICROHABITAT									
In water	80	20	10*	83	17	6	100	0	8*
On Rock in Water	92	8	37**	94	6	17**	93	7	41**
On Rock on Bank	27	73	214**	34	66	67*	34	66	66*
On Bank	13	87	80**	30	70	31*	34	66	90*
ORIGINAL ORIENTATION									
Facing Water	43	56	99	—	—	—	60	40	69
Parallel with Shore	35	65	63**	—	—	—	46	54	61
Facing Bank	14	86	82**	—	—	—	36	64	61*
DEGREE CHANGE IN ORIENTATION									
0°	25	75	107	—	—	—	48	52	56
45°	39	61	28	—	—	—	57	43	14
90°	34	66	61	—	—	—	53	47	59
135°	31	69	18	—	—	—	33	67	16
180°	19	81	43	—	—	—	39	61	37

An asterisk at N values for Microhabitat and Original Orientation categories indicates a chi-square test on the actual numbers gave a P of<0.05 (significant). Two asterisks indicate P< 0.001 (highly significant). No asterisks indicate P>0.05 (not significant).

TABLE 7. The exercise capacities of adult and juvenile *Eulamprus quoyii*.

		TEMPERATURE (°C)		ADULTS				JUVENILES			
EXERCISE	UNITS	Air	Medium	Mass (g)	Snout-vent length (mm)	n	Time	Mass (g)	Snout-vent length (mm)	n	Time
DIVING											
Mean	s	31.6±1.1	19.1±0.7	24.6±1.5	102.9±1.5	14	360.5±17.3	7.3±0.6	69.7±1.6	7	312.7±11.0
Max.	s						1075.1± 182.5			6	83.9±59.8
SWIMMING SPEED											
Mean	ms^{-1}	31.6±1.1	22.1±1.4	23.4±1.5	102.0±1.9	12	0.64±0.01	0.8±0.1	34.4±1.0	5	0.29±0.01
Max.	ms^{-1}						0.85±0.07				0.36±0.02
SWIMMING STAMINA											
Trial 1											
Mean	s	31.6±1.1	19.8±2.1	25.9±1.7	103.0±1.8	10	130.1±2.0	7.3±0.6	69.7±1.7	6	118.7±3.8
Max.	s						155.8±0.1				154.3±6.5
Trial 2											
Mean	s	31.6±1.1	19.8±2.1			10	74.6±1.8			6	59.0±2.4
Max.	s						93.9±0.1				70.0±10.7
RUNNING SPEED											
Mean	ms^{-1}	31.6±1.1	31.6±1.1	23.4±1.5	102.0±1.9	12	0.96±0.01	0.8±0.1	34.4±1.0	5	0.39±0.02
Max.	ms^{-1}						1.17±0.05				0.54±0.06
RUNNING STAMINA											
Trial 1											
Mean	s	31.0±1.0	18.1±0.8	25.8±2.8	105.0±3.0	5	114.5±2.3	7.3±1.0	67.8±1.9	4	106.2±2.6
Max.	s						129.4±5.0				125.0±9.2
Trial 2											
Mean	s	31.0±1.0	18.1±0.8			5	79.5±1.9			4	67.5±.2.0
Max.	s						93.6±2.9				86.8±7.1

sibility is that this species adjusts its escape tactic to a particular kind of potential predator, e.g. using different tactics for snakes than for birds, or for humans. By using only one stimulus (humans) we may have observed only the subset of escape tactics given to large land animals. Analysis of predator-specific escape responses might be a fruitful line of research.

We would like to caution against over-interpretation of such diversity indices. The index is influenced by the number of categories of escape response. Had we used each of our rock sizes as a separate category (Table 1) rather than 'rocks' as a single one, the diversity index would have been altered. We suggest that some of the variation in escape diversity may merely reflect differences in investigator's classifications of escape tactics.

The utilisation of water by primarily terrestrial lizards for predator avoidance is not uncommon, being practised by over 50 species from 10 families (Daniels, 1984a). Most of these lizards swim across open water to avoid terrestrial predators. A number submerge and rest on the bottom until a predator departs. Water skinks utilise short aerobically sustained dives (Daniels, 1984a). The predator may still be in the vicinity when the lizard emerges, but because the skink is not exhausted it can submerge again if threatened. Moreover, because anaerobiosis has not been extensively employed, the skinks are still capable of rapid swimming to avoid predators. Thus, short dives keep all escape options open. In addition, the use of swimming, diving and/or running in sequence has the advantage of providing flexibility if one method of escape is suddenly unavailable. For example, if disturbance of rock cover removes running or other terrestrial tactics as a viable escape method, swimming or diving still remain.

The second major tactical advantage concerns locomotor capacity. Water skinks can dive for up to 35 minutes and swim or run continuously for over 2 minutes. However, in natural situations, these lizards either do not, or do not have to, perform at these maximal capacities. By exhibiting dives of 2-5 minutes and sprints of 2 seconds in the field, water skinks are utilising only a small proportion of their maximal escape capability. Such behaviour enables the lizards to avoid a potential predator in a given encounter and still be able to resume normal daily activities (or flee from other predators) almost immediately. These lizards have flexibility in escape tactics and the behavioural and locomotor capacity to maximise the effectiveness of any of the escape tactics selected.

INTRASPECIFIC DIFFERENCES

Ontogenetic changes in diving performance have been observed in several ectotherms and Butler and Jones (1982) suggested that dive duration should be proportional to (body mass)$^{0.25}$ for ectotherms. The values obtained on water skinks in the present study are consistent with that view. Ontogenetic increases in swimming speed have been observed for *Amblyrhynchus cristatus* (Bartholomew et al., 1976) and some anurans (Taigen and Pough, 1979; Miller, 1983). Running speed increases ontogenetically for several African lizards (Huey, 1982; Huey and Hertz, 1982). The swimming stamina and recovery capacity of juvenile water skinks was much lower than that of adults, although the running stamina of the two size groups were similar.

In view of the lower capabilities of juveniles for aquatic life it is surprising that their escape responses did not differ significantly from those of adults. However, use of water for escape is low in all age groups, and even the adults have not developed unusual physiological adaptations for diving (Daniels, Oakes and Heatwole, 1987).

EFFECT OF HABITAT ON ESCAPE TACTICS

E. quoyii is a territorial, solitary heliotherm. Sunlit rocks, especially those on a soil substrate suitable for burrowing, are the preferred microhabitat for basking and other activities (Spellerberg, 1972a,b,c,d, 1974; Done and Heatwole, 1977). Because of their close proximity to rocks and their use of them for other activities, it is not surprising that water skinks also use rocks as a primary shelter during escape.

Schall and Pianka (1980) observed that the escape diversity of *Cnemidophorus* was not correlated with environmental heterogeneity (plant volume diversity or percent vegetative cover) but rather with presumed predation pressure (high incidence of tail breaks). Aside from the doubtfulness of incidence of broken tails as an indicator of predation pressure (e.g. intraspecific fighting also may injure tails), such an explanation cannot be used to explain the differences in escape diversity between Blue Hole and Boorolong Creek lizards in the present study. Samples from both sites had similar frequencies of animals with regenerated tails; Blue Hole, original tails 54%, regenerated tails 46% (N = 15); Boorolong Creek, original tails 55%,

TABLE 8. Diversity of escape tactics and the practice of immobility by lizards.

Species	Habitat	Escape Tactic Diversity	Techniques for Predator Avoidance	Number of Classes	n	Frequency of Remaining Motionless	References
*Anolis aeneus** juveniles	Terrestrial	2.80	MR	3	23	0.44	Stamps (1983)
Cnemidophorus (overall)	Terrestrial	9.04	MR	12	–	–	Schall & Pianka (1980)
C. exsanguis	Terrestrial	7.2	MR	12	155	0.15	Schall & Pianka (1980)
C. gularis	Terrestrial	8.2	MR	12	169	0.05	Schall & Pianka (1980)
C. inornatus	Terrestrial	6.5	MR	12	268	0.16	Schall & Pianka (1980)
C. tesselatus	Terrestrial	6.5	MR	12	143	0.15	Schall & Pianka (1980)
C. tigris	Terrestrial	4.4	MR	12	288	0.03	Schall & Pianka (1980)
Eulamprus quoyii	Aquatic Terrestrial	4.31	MRSD	10	698	0.07	This Study
*Lacerta vivipara**							
males	Terrestrial	3.14	MR	6	401	0.01	Bauwens & Thoen (1981)
females	Terrestrial	3.12	MR	6	475	0.01	Bauwens & Thoen (1981)
Liolaemus fuscus	Terrestrial	1.32	R	2	297	–	Jaksic & Núñez (1979)
L. lemniscatus	Terrestrial	1.39	R	2	148	–	Jaksic & Núñez (1979)
Lygodactylus capensis	Arboreal	7.91	MRJ	10	100	0.07	Simbotwe (1983)
L. chobiensis	Arboreal	8.27	MRJ	10	100	0.07	Simbotwe (1983)
Physignuthus lesueurii	Terrestrial/ Aquatic	4.42	RSD	10	870		Daniels (1984a)

M = remain motionless. J =jump (from tree to tree). R = run. S = swim. D = dive. * = values calculated from data presented in the paper.

regenerated tails 45% (N = 22). These frequencies are not significantly different ($G_{(1)} = 0.04$, $P>0.05$) between the two areas.

Contrary to the prediction of Schall and Pianka (1980), mode of escape was related to the physical characteristics of the habitat. Blue Hole was the rockiest site and a greater proportion of water skinks there escaped to rocks than at any other locality. There was a significant increase in the utilisation of aquatic escape tactics from the rocky to the vegetated sites and from the fast-flowing to the slow-flowing sites. It appears that if rock cover is available, then lizards prefer to run to it rather than utilise aquatic escape behaviours. Running to rocks may represent the energetically least expensive form of escape because the sprint distance is frequently short and rocks represent a secure form of protection. Moreover, diving into cold water results in decrease in body temperature which may retard locomotor capacity (Hertz et al., 1982; Daniels, Heatwole and Oakes, 1987). Fast stream flow may pose the threat of sweeping the lizard away and probably requires greater energy expenditure during swimming.

In conclusion, water skinks alter their escape tactics depending on their immediate location and orientation and the physical characteristics of the habitat, and seem to select the energetically least demanding option. As a result they use only a small part of their capacity in a given escape attempt, leaving sufficient reserves for repeated attempts, or for other activities.

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AN INEXPENSIVE FORCE PLATFORM FOR USE WITH SMALL ANIMALS: DESIGN AND APPLICATION

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A force platform was designed and manufactured to meet the following criteria. 1. be inexpensive and able to be constructed from readily available components. 2. be suitable for use with animals of less than 1kg and able to to provide an indication of the direction and timing of the forces produced by a lizard during locomotion. 3. be small enough to record forces from a pair of ipsilateral feet only, but large enough to allow a reasonable chance for a running lizard to place its feet on the platform.
A force analysis of Bearded Dragons (*Amphibolurus barbatus*) and Water Dragons (*Physignathus lesueurii*) indicated that unlike the more erect mammals, the legs of lizards apply no forward force to the ground during the limb cycle. Instead of the acceleration/deceleration cycle that occurs in the limbs of erect mammals, the lizards apparently apply a 'rotational' force that simply alters the angular momentum of the limb. These findings are discussed. ☐ *Lizards, locomotion, force platform.*

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The locomotor performance of animals can be investigated in a number of different ways: trackway analysis, for example, can provide estimates of speed, stride length, animal size etc. even for animals that have long been extinct (Thulborn, 1982; Thulborn and Wade, 1984); anatomical studies can elucidate certain locomotor constraints (e.g. Russell and Rewcastle, 1979); and kinematic analysis has been used to provide comparative data useful in understanding locomotor abnormalities (Parker and Bronks, 1980). However, none of these methods can provide more than an estimate of the way in which forces are transmitted to the ground during locomotion; to measure these ground reaction forces, a force platform is required. Unfortunately, force platforms are not always readily available, are often complicated, sometimes not completely suitable and usually extremely expensive. In this paper I describe a force platform that was used as part of a larger study of the locomotion of two species of agamid lizard. The platform is cheap, simple to construct and suitable for use with small animals.

THE FORCE PLATFORM

DESIGN CRITERIA

To produce an inexpensive force platform that could be constructed from readily available components, was suitable for animals less than 1kg, and would provide an indication of the direction and timing of the typical forces produced during the locomotion of the lizards used in this study. The platform was to be small enough to record forces from a pair of ipsilateral feet only, but big enough to allow a reasonable chance for a running lizard to place its feet on the platform.

TRANSDUCER ELEMENTS

The most expensive components of a force platform are the transducer elements used to convert variations in the applied forces into signals that can be recorded and analysed. In the system described here, inexpensive, commercially-available crystal microphone elements were modified (Fig. 1 and see below) to act as force tranducers. The output from these crystal elements varies with the rate of change of the force (i.e. the first derivative of the force, Fig. 2) thereby making an estimation of the actual value of applied forces an integrating process (either electrical or mathematical). However, as the primary purpose of the force platform was to provide an indication of the direction and timing of the forces applied to the ground by a moving lizard, actual values of the forces were not required and integration of the crystal output was considered unnecessary.

CONSTRUCTION (Fig. 3)

The surface plate for the force platform was